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Abstract

The Creek Town mangrove swamp occurs at the saline/fresh water interface within the ever-wet humid tropical zone of Southeastern Nigeria. A survey of the swamp was undertaken to map the mangrove physiographic habitats, and to obtain vegetation and environmental measurements. Due to the dynamic nature of the swamp landscape, several physiographic mangrove habitats have evolved. Habitat differences relate to swamp gradient, salinity variation, substrate texture and carbonate content of the soil. Species presence and abundance vary between the habitats. Diurnally flooded tidal creek and distributary wetlands are dominated by *Acrostichum aureum* and *Nypa fruticans* in association with *Rhizophora* spp. and *Avicennia africana*. *Raphia* spp. and *Vossia cuspidata* which are upland forest species have invaded the supratidal and hinterland levee habitats due to increasing salinity tolerance and competitive abilities. Vegetation zonation is apparent from the channels inland but there are quirks in the zonation pattern due to variations in local topography within the species zones. The environmental conditions and species distribution are similar to other transitional mangroves of the West Africa–Americas Mangrove Formation. © 1997 Elsevier Science B.V. All rights reserved.

Keywords: mangrove vegetation; habitat; environment; soil; physiography; salinity

1. Introduction

The term mangrove generally applies to an association of trees which live in wet, loose soils in tropical and temperate tide waters. The term also applies to the species of plants which occur in such an association. The occurrence of mangroves (*Rhizophora mangle* — G. F. May, *Rhizophora racemosa* — G. F. May, *Rhizophora harrisonii* — R. Keay and *Avicennia africana* — Moldenke), commonly codominant species with *Nypa fruticans* (Thumb.), *Raphia vinifera*, *Raphia hookerii* (Linn) and *Phoenix rechinata* (Jacq.) in the brackish/saline estuarine forests of southeastern Nigeria reach their

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northernmost limits in the Creek Town swamp. Two classes of plants make up the mangrove vegetation of this area: (i) Genera and higher taxa found only in the mangrove habitat, and (ii) species that belong to genera of upland plants but which have became adapted to life in the mangrove habitats. The mangrove swamp landscape is dynamic. Due to salinity variations, tidal flooding, channel deposition and abandonement and downwarping of sediments, several landforms have evolved which favour establishment and growth of different mangrove species (Ukpong, 1992a). The present study represents an ecological investigation of marginal mangroves occurring at the transitional zone where oceanic influences and fresh water inputs from upland streams are equally felt. The objectives of the study are:

1. To identify the physiographic habitats associated with mangrove growth using environmental variables as indicators, and
2. To compare the composition and abundance of species among the physiographic habitats.

2. The study area

The Creek Town mangrove swamp is located between latitudes 4°55′N and 5°00′N, about 20 km from the Atlantic Ocean coast (Fig. 1). North of 5°00′N, mangrove growth diminishes and transits into the fresh water swamp forest as a consequence of diminishing salinity and tidal influence. Vegetation development in the area is favoured by a humid tropical climate with abundant rainfall (4021 mm per annum) distibuted throughout the year. Rainfall peaks occur in July/August (1200 mm) while lowest values are observed in December/February (180 mm). The mean annual temperature is 27°C, with a relatively small annual range of 5°C. Relative humidity averages 80%. The Mean Sea Level tidal range (MSL) is 1.95 m for the Creek Town/Calabar River area. Relative to the MSL, the Mean High Water Spring (MHWS) is 3.05 m, while the Mean Low Water Neap (MLWN) is 1.04 m (Nigerian Navy, 1991). The mean tidal amplitude in the Calabar River is 1.01 m at spring tides and 0.81 m at neap tides (Ramanathan, 1981).

3. Methods

A survey of the Creek Town mangrove swamp was undertaken with the aim of identifying and mapping the fluvial physiographic units on which mangrove vegetation occurs. Aerial photographs (scale 1:5,000) of the study area were also used in the investigation of vegetation distribution and zonation patterns. Physiographyic habitat boundaries were delimited in the field and compared with aerial photograph overlays. The morphology of the habitats was described in terms of gradient, elevation and relationship to tide levels. Elevation was estimated with an Abney Level along transects while tide relations were made with reference to Tide Tables (Nigerian Navy, 1991). In each habitat vegetation >3 m tall was sampled in ten random 15×15 m quadrats. Vegetation between 1 and 3 m tall and <1 m were sampled in 5 m^2 and 1 m^2 subquadrats respectively. Occurrences of species outside the quadrats were noted.

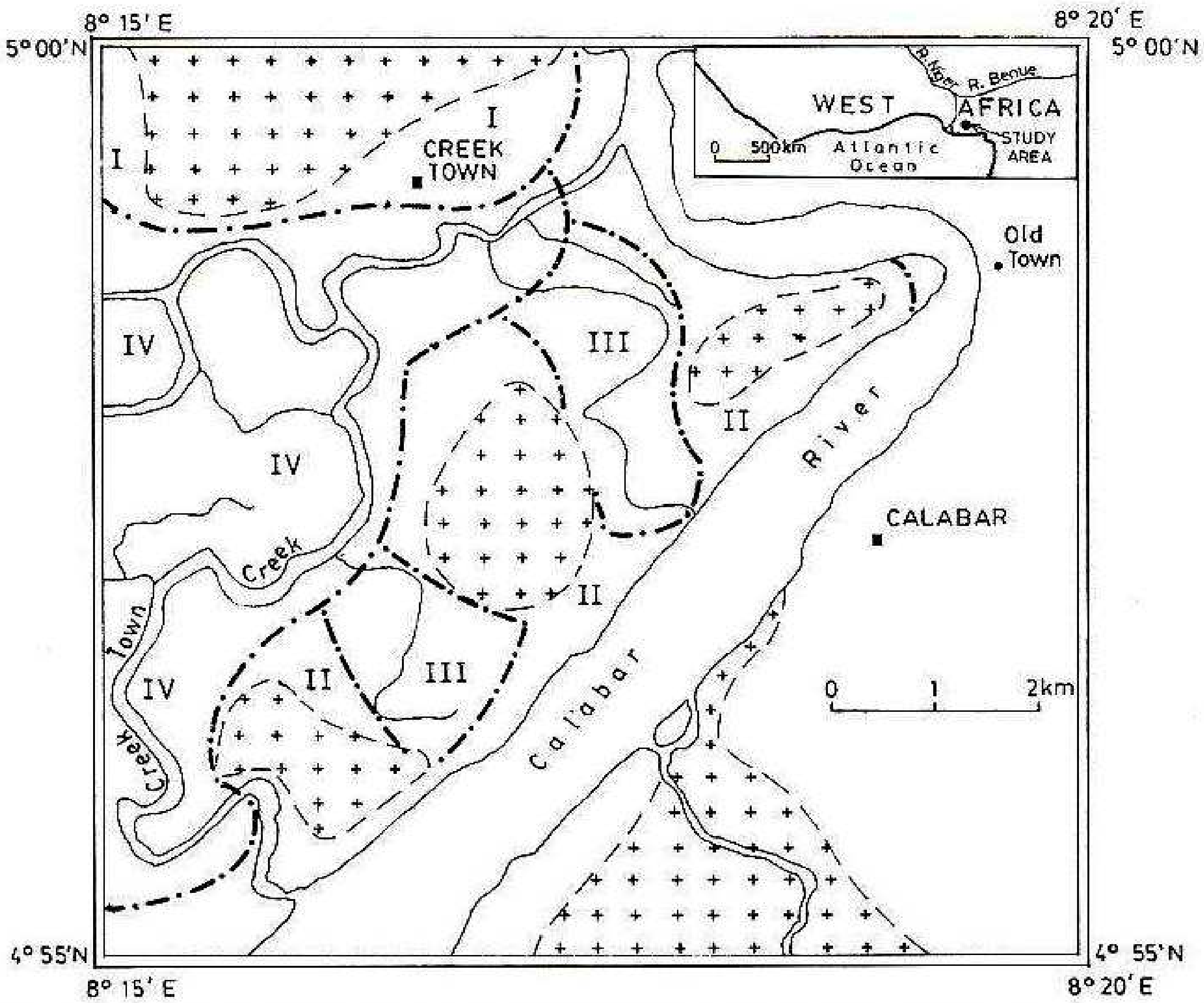

Fig. 1. Map of Creek Town mangrove swamp showing location in West Africa (insert): + + + = non-Mangroves on elevated segments. I = supratidal dunes, II = hinterland levees, III = distributary channel wetlands, IV = tidal creek wetlands.

Coverage–abundance estimates of all species within each habitat were obtained based on the Domin ± 10 scale (Kershaw, 1980). Species nomenclature followed Keay (1953), Savory (1953) and Tomlinson (1986).

Each environmental measurement in a quadrat consisted of four observations, bulked for labartory analysis. Soil water salinity was measured at the water table in the swamp using a portable refractometer calibrated against a Bisset Berman salinometer. Other measurements were obtained for a soil depth of 0–30 cm. Particle size composition was analysed by the hydrometer method (Bouyoucos, 1962). Bulk density was determined on cores (Blake, 1965) collected from 0–15 cm and 15–30 cm layers. Carbonate content was determined by the Bromo Thymol Blue titration method (Jackson, 1962) and calculated as calcium carbonate (g/100 g) oven dry soil; organic carbon by the Walkley–Black method and pH potentiometrically using a soil to water ratio of 1:2. An analysis of variance was used to separate variation in environmental properties among the mangrove physiographic habitats.

4. Results

4.1. Habitat morphology

The supratidal dunes (Fig. 2, I) occur at the most landward portions of the mangrove swamp, forming an ecotone between the frequently flooded segments and the upland forests (see Fig. 1). The dunes are not continuous but are separated into ridges by ebbflood channels. Mangrove species occur along these ebbflood channels, but in terms of complexity the mangroves are insignificant. The dunes are abandoned levees where sedimentation within former creek channels had diverted flow to areas of lower gradients. The highest gradients (≥ 0.004) occur in the supratidal areas, flooded infrequently at NHWS which is the highest mean tide in the Creek Town channel. The dunes generally lie 2 m above MSL.

Hinterland levees are of lower elevation than supratidal dunes, being of more "recent" origin. Gradients are 0.002–004. The levees are aligned parallel to abandoned water channels which contain numerous silting ponds (Fig. 2, II). The levees, have variable width, and where the supratidal dune is absent, may merge inshoreward into the low fresh-water swamps. Some portions of the levees exceed 2.5m in height. The habitat is flooded frequently by tides lower than MHWS but higher than MSL.

Where distributary channels traverse the swamp, a distinctive mangrove habitat has evolved (Fig. 2, III). Some of the distributary creeks display evidence of silting, abandonment and infilling of recent mander scars.

Tidal creeks and associated channels are of variable width and depth, bordered by prominent levees. Behind the levees, horizontal surfaces have gradients ≤ 0.004 and grade inland into the distributary channel habitats. Tidal creek wetlands are flooded at MLWN (Fig. 2, IV), below MSL. Tidal influence is strong since the creeks have a direct link with the Atlantic via the Calabar River.

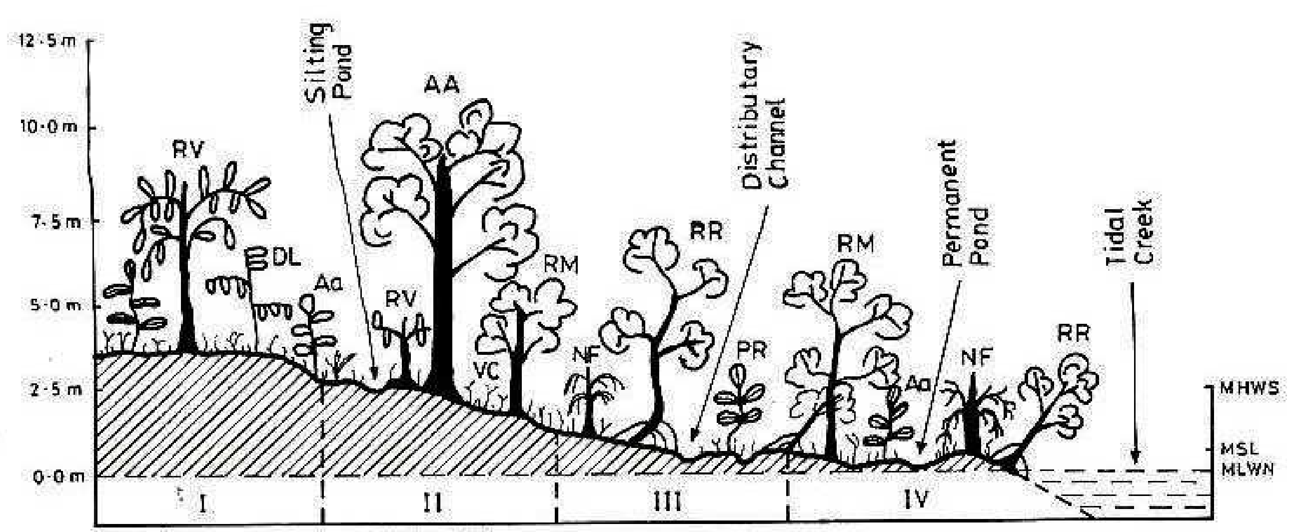

Fig. 2. Diagramatic comparison of the morphology of mangrove habitats: I = supratidal dunes, II = hinterland levees, III = distributary channel wetlands, IV = tidal creek wetlands.

Table 1
Particle size composition and bulk density data of the soil (values are means ± SE)

Physiographic habitats	Sand (%)	Silt (%)	Clay (%)	Bulk density (g/cm^{-3})
I. Supratidal dunes	64.5 ± 8.3	22.4 ± 2.5	13.1 ± 1.8	0.93 ± 0.15
II. Hinterland leavees	62.3 ± 5.4	26.2 ± 43	11.5 ± 1.6	0.88 ± 0.15
III. Distributary wetlands	56.3 ± 6.5	36.4 ± 2.7	6.9 ± 2.1	0.73 ± 0.18
IV. Tidal creek wetlands	44.2 ± 8.4	48.6 ± 3.6	7.2 ± 1.5	0.70 ± 0.14
	* [a]	*	ns	*

[a] * Difference between means significant at 1% confidence level; ns = not significant.

4.2. Habitat–environmental relations

The physiographic mangrove habitats are landform units formed through varying geomorphic processes, including transportation and deposition of sediments by channel flow, channel abandonment and subsidence. Since the intensity of these processes varies, the substrates also show variation in particle size distribution although the sediments may have developed and transported from similar sources.

Apart from the tidal creek wetland which has a silty loam soil, other habitats have a sandy loam texture (Table 1). High sand content, for example in the supratidal and hinterland levee soils indicates the predominance of terrestrial over tidal sediments. The sandy loam texture correlates with relatively high bulk densities. In mangrove swamps, high bulk densities have been associated with sandy soils (Naidoo, 1980). Silt fractions are relatively high in the tidal creek and distributary channel soils due to regular diurnal flooding and active deposition of water-borne sediments. The finer clay fractions are regularly churned and flushed out of the swamp by retreating tides.

Table 2 shows that tidal flooding accounts for salinity variations between the habitats. Regularly flooded habitats (II and IV) have the highest soil water salinities in the dry season (January). In the wet season (July), the mangrove habitats are relatively fresh. The supratidal dunes and hinterland levees are the least saline due to proximity to overland freshwater and subsurface seepage.

Carbonate contents of soils are appreciably lower in the tidal creek and distributary channel wetlands than in the supratidal dunes and hinterland levees (Table 3). These

Table 2
Soil water salinity data (values are means ± SE)

Physiographic habitats	Salinity (‰)		
	January	July	October
I. Supratidal dunes	36.2 ± 0.2	3.4 ± 0.2	13.6 ± 0.2
II. Hinterland levees	36.6 ± 0.4	3.8 ± 0.2	15.6 ± 0.1
III. Distributary wetlands	44.4 ± 1.6	3.3 ± 0.1	18.5 ± 0.3
IV. Tidal creek wetlands	61.4 ± 3.6	2.2 ± 0.4	21.4 ± 0.5
	* [a]	ns	ns

[a] * Difference between means significant at 1% confidence level; ns = not significant.

Table 3
Carbonate, organic carbon and pH data (values are means ± SE)

Physiographic habitats	CO_3^- (g/100 g)	Organic C (%)	pH (field moist)	pH (air dry)
I. Supratidal dunes	13.8 ± 2.7	4.2 ± 0.9	6.2 ± 0.1	4.8 ± 0.2
II. Hinterland levees	14.5 ± 1.9	5.8 ± 1.8	6.2 ± 0.1	4.7 ± 0.1
III. Distributary wetlands	9.8 ± 3.2	9.4 ± 2.6	5.7 ± 0.2	3.4 ± 0.1
IV. Tidal creek wetlands	7.5 ± 2.5	9.6 ± 1.5	5.7 ± 0.2	3.2 ± 0.0
	** [a]	*	ns	*

[a] ** Difference between menas significant at 1% level; * significant at 5% level; ns = not significant.

values suggest that the soils may have been derived from varying sources. Organic carbon content varies significantly across the habitats. The highest values are associated with tidal creek and distributary channel wetlands. The high values correlate with increasing soil acidity, indicated by pH. Soils of the infrequental inundated habitats (I and II) are moderately acid. High organic carbon levels in mangrove swamps have been associated with tidal imports of organic materials and a slow rate of silting due to low gradients (Moorman and Pons, 1974).

Variation of soil properties reflects the influences of groundwater seepage and the response of the parameters to tidal flushing of the surface soil. Where the habitat is a basin wetland, for example the distributary creek habitat, flood waters are often trapped behind the narrow channel levees and in silting ponds. Thus, while the levees may have better drainage, the depressions behind the levees have impaired drainage. Areas with impaired drainage may be relatively stable in terms of salt accumulation since subsurface seepage is considerably reduced.

The hinterland levee and supratidal dune habitats are particularly influenced by elevational diiferences between the shores and the uplands. With a higher topography in the proximity of the high forest it seems obvious that soil properties fluctuate between wet and dry spells of the local climate. During wet spells, overland inputs transporting terrigeneous sediments from the forest zone may be significant, while during dry spells, the lower water table increases the rate of absorption of saline tides at the swamp surface.

4.3. Mangrove communities

Table 4 shows that on the supratidal dunes *Raphia vinifera* is the leading dominant species with *Acutas afer*, *Raphia hookerii* and *Drepanocarpus lunatus* as important associes. The abundance of *R. vinifera*, basically a fresh water species reflects adaptation to a brackish environment. The last landward limits of the dunes are occupied by *Elaeis guineensis*, a true high forest species. On the hinterland levees, upland freshwater sedges, for example *Vossia cuspidata* and *Triumfetta rhomboideae* are associated with tidal swamp species, for example *Acrostichum aureum*, *Cyperus* spp., *Rhizophora mangle* and *Avicennia africana*. The upland species have invaded these habitats due to increasing salinity tolerance and competitive ability.

The distributary channel wetland supports a *Nypa fruticans* community. The important associes are commonly identified with tidal mangroves, for example *Rhizophora*

Table 4

Summary of species synthetic characteristics in four physiographic mangrove habitats. I = Supratidal dunes, II = hinterland levee, III = distributary channel wetlands, IV = tidal creek wetlands. *A* = Number of habitats in which species is recorded; *B* = number of habitats in which species has presence estimate 50% or more; *P* = % presence; Ab = abundance estimate according to Domin ± 10 scale (Table 5)

Species (trees)	I		II		III		IV		*A*	*B*
	P	Ab	*P*	Ab	*P*	Ab	*P*	Ab		
1. *Nypa fruticans*			10	1–2	100	5–10	70	2–5	3	2
2. *Raphia vinifera*	100	5–7	50	1–3	20	+ –1			3	2
3. *Rhizophora racemosa*	10	1–2	10	+ –3	90	5–8	70	2–5	4	2
4. *Rhizophora mangle*	10	1–2	60	+ –5	40	+ –4	60	+ –4	4	2
5. *Avicennia africana*	10	1–3	50	1–4	80	2–5	10	1–2	4	2
6. *Phoenix reclinata*			10	1–2	50	2–5	30	+ –3	3	1
7. *Raphia hookerii* (Sedges)	60	+ –5	30	+ –3	10	+			3	1
8. *Drepanocarpus lunatus*	50	+ –3	10	+	10	1	10	+	4	1
9. *Cyperus papyrus*	10	+	20	1–3	40	+ –5			3	
10. *Conocarpus erectus*	10	1–2	70	1–4	10	+ –2			3	1
11. *Triumfetta rhombiodeae*	50	1–3	20	+ –3					2	1
12. *Pandanus candelabrum*	10	+	20	+ –1			30	+ –4	3	
13. *Acutas afer*	50	+ –4	10	+ –3	20	+ –1			3	1
14. *Ipomeoa cairica*	50	1–4	10	+					3	1
15. *Cyperus articulatus*	30	1–3			50	1–3	10	+ –2	3	1
(Grasses/Ferns)										
16. *Vossia cuspidata*	10	+ –1	80	5–7	10	1–3			3	1
17. *Acrostichum aureum*	50	1–5	60	3–4	70	2–5	100	5–7	4	4
18. *Sesuvium portulacstrum*	50	1–7	40	+ –4	50	2–3			3	2
19. *Paspalum vaginatum*	10	+ –1	30	+ –3			10	+	3	
20. *Imperata cylindrica*	10	+	10	1–2			10	+ –1	3	
Species present in one physiographic habitat										
21. *Diodea maritma* (II)			10	+ –2						
22. *Portulaca folliosa* (II)			50	1–4						
23. *Sporobolus virginicus* (II)			30	1–3						
24. *Panicum maximum* (I)	10	1–2								
25. *Phyllanthus amarus* (II)			10	1–2						
26. *Chrysobalanus orbicularis* (II)			10	+						
27. *Dononia viscos* (I)	10	2								
28. *Euphorbia glaucophylla* (I)	40	+ –2								
29. *Acathus ebracteatus* (I)	10	1–2								
30. *Bravaisia tubiflora* (I)	10	1								
31. *Mutingia calabura* (I)	10	2								
32. *Fimbristylis obtusifolia* (I)	10	2								
33. *Selaginella* spp. (II)			10	2						
34. *Ripogonun* spp. (I)	30	2–4								

racemosa, *Avicennia africana*, *Phoenix reclinata*, *Acrostichum aureum* and *R. mangle*. Diurnally flooded estuarine mangrove swamp is typified by the tidal creek wetland where upland species are usually absent; *A. aureum* forms a community type with *N. fruticans*, *R. racemosa* and *R. mangle* as the most important associes.

Table 5
Domin ± 10 scale

Scale	Cover%
10	100
9	75–100
8	50–75
7	33–50
6	25–33
5	10–25
4	5–10
3	1–5
2	<1
1, +	Insignificant, solitary cover

4.4. Vegetation zonation

Aerial photograph interpretations and ground truth support the idealized zonation pattern shown in Fig. 3. Zonation of upland species, for example *Raphia* spp.; *T. rhomboideae* and *Ipomoea cairica* tend to correlate with regular tidal limits while zonation of true species, for example *Rhizophora* spp. and *N. fruticans* are less distinct. Zonation is sparper on the hinterland levees and supratidal dunes than on the other habitats. Generally, the mangroves are organized into zones following the water channel (Fig. 3). Each zone is often occupied by one mangrove community or by a combination of more than one community types. Two major zones of vegetation transition are apparent:

(a) The brackish channel segments dominated by *N. fruticans* and *Rhizophora* spp., usually succeeded by *A. africana* and *P. reclinata* in association with *A. aureum* and *Paspalum veginatum* (SW.) on the elevated levees and,

(b) The freshwater/brackish zone where *R. vinifera, V. cuspidata* and *Acutas afer* occur with salt - tolerant ferns and sedges, for example *A. aureum*. *Ripogonun* spp. and

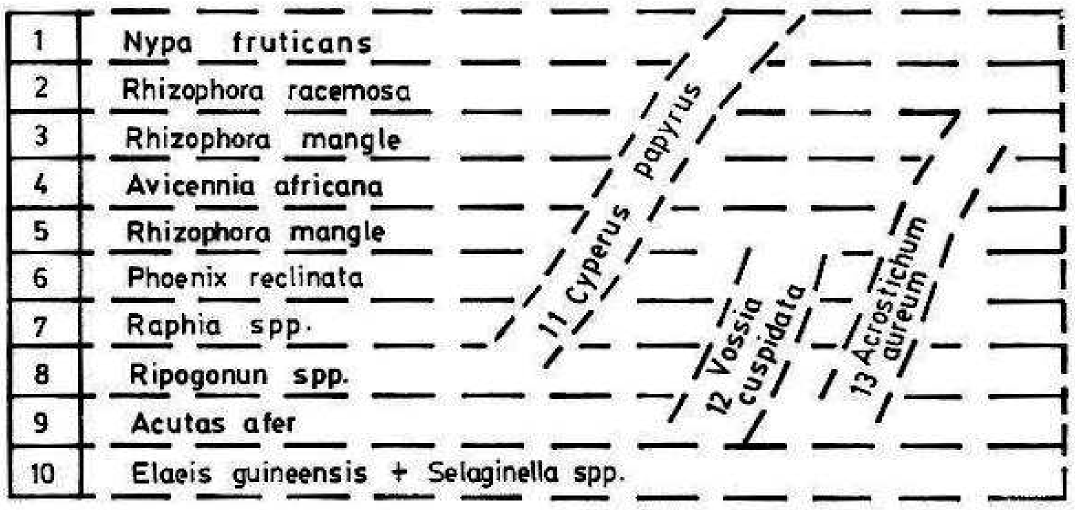

Fig. 3. Idealized species zonation pattern in the mangroves. (1)–(10) Sequence of species occurrence from the shorelines and channels inland to the lowland forest. (11)–(13) Species associated with microtopographic variations (depressions and mounds) across the major species zones.

T. rhomboideae are ecotonal, occurring behind *R. vinifera* stands at the upland forest margins. The upland forest fringes are dominated by *Elaeis guineensis*. The influence of microtopographic variations is most marked with respect to the ferns and sedges. While the water table occurred at the surface in microdepressions where *Acrostichum aureum* and *Cyperus papyrus* occurred, it was much lower (< 40 cm) in mound positions dominated by *Vossia cuspidata*, *Acutas afer* and *Selaginella* spp.

5. Discussion and conclusion

The establishment and development of mangrove vegetation is tied to swamp landscape evolution. Hence mangrove physiographic habitats and communiy types which relate to landscape morphology can be recognized in the field (Lugo and Snedaker, 1974). Thom (1967) had discussed these physiographic relations, together with the hypothetical sequence of mangrove habitat evolution. The present study has indicated that indeed the distribution of mangrove vegetation is influenced by topographic variations arising from the active processes of sedimentation and channel abondonment. The mangrove swamp sediments are composed of soft sandy or silty mud. The predominance of siliceous and quartizitic sands ($44.2 \pm 8.4\%$–$64.5 \pm 8.5\%$) is due to the terrigeneous nature of the sediments (see Table 1). Hence sediment accretion is regulated by physiographic–geomorphic factors which include the rate at which sediment is brought into the swamp by rivers and tides and swamp elevation relative to the upland which determines the effectiveness of overland flow to transport coarse sand across the supratidal dunes (see Fig. 2).

The major distinguishing characteristics of the mangrove habitats relate to:

(a) Tidal levels and swamp gradient which determine the extent and duration of flooding. A high tidal range excludes competion from non-mangroves and is a prequisite for the optimum growth of monodominant species (Semeniuk, 1980). A low swamp gradient enables a wide belt of mangroves to be established across mudflats. The mangrove props and aerial roots aid entrapment of debris and sediments, leading to: (i) Constriction, silting and abandonment of water channels and (ii) Increase in swamp elevation and variation in microtopography from the channels inland;

(b) Salinity gradient which determines species tolerance limits and composition of community types. Mangroves are halophytic in nature although the salinity range within which they occur varies greatly. The interannual variability is wide, being related to normal climatic shifts from wet to dry periods. Consequently, near the upland ecotone, fresh water species, for example *R. vinifera* and *V. cuspidata* are able to compete and dominate the mangroves.

The salinity gradient leads to the establishment of interface consocies on sub-habitats where mangroves and non-mangroves show equal adaptation.

(c) Carbonate levels, from which the origin of habitat sediments may be inferred. Carbonate content has been noted to be high in mangrove soils, perhaps, due to the large molluscan population usually associated with saline or brackish swamps (Kassas and Zahran, 1967), and to the precipitation of calcuim carbonate along the fresh/salt water mixing zone. In this study, it is hypothesized that the hypersalinity of soil water in the dry season (see Table 2) would generate a net flow of sea water to upstream, thus bringing oceanic calcium carbonate to the mangroves. Wolanski (1995) noted that the calcium carbonate acts as a silt and clay sediment trap, resulting in the observed pattern of sediment coarsening with distance from the creeks (E. Wolanski, pers. commun., 1995) (see Table 1). In such a hypersaline/fresh water interface, *Rhizophora* spp. often dominates (Walsh, 1974). In Nigeria, *Rhizophora* spp. at this interface, being inferior competitors have been gradually replaced by the versatile *Nypa fruticans* (Ukpong, 1991). Based on the classification by Scholl (1963), the Creek Town mangrove swamp is an allochthonous swamp since it receives abundant sediments from creeks and tidal channels flowing from outside the environmental framework of the swamp.

While some species occurrences are restricted to one habitat (Table 4), several species (*R. racemosa*, *R. mangle*, *A. aureum*, *A. africana*, *D. lunatus*) occur in all habitats, reflecting overlap in environmental and soil conditions or overlapping tolerance of stress factors, for example salinity variations and tidal flushing. Species abundance indicates the habitats on which the species compete effectively and share niche relations to the changing environment. A mixed mangrove community where there is no clear species dominance is represented on the hinterland levee. These mosaics of minor community types result from microtopographic variations in mangrove habitats (Ukpong, 1992b) and may create aberrants or quirks in the zonation pattern (Rabinowitz, 1978). Microtopographic control over specise distribution is related to sediment profiles that are alternately, reduced and oxidized due to variable tide and water table levels. Hence the mosaics relate to microtopographic mounds and depressions in the communities. These dynamic relations between microtopography and plants are influenced by strong periodic forces, including sediment accumulation from the upland forest zone during the rainy season, tidal sorting of sediments and variable accumulation of wrack by tides. Salinity fluctuation due to freshwater inputs also determines which species establish on mound or depression positions. The intensity of these forces varies between the community types. Although most species are capable of adapting to the rigorous conditions, microtopographic differences constitute an important geomorphological factor in the distribution of the species.

The Creek Town swamp represents the northernmost limits of mangrove growth in southeastern Nigeria. Similar transitional environmental conditions and species niche relations were reported in the Gambia by Giglioli and Thornton (1965). Semeniuk (1983) in Australia had shown that transitional mangroves could arise due to regional/local freshwater seepage into the saline zones. Moorman and Pons (1974), in Surinam, analysed the soils along an interface/transitional zone and proposed an agricultural land use scheme for the swamps. These transitional habitats constitute mixed woodland mangroves in the physiographic classification of Davy (1938) and Lugo and Snedaker (1974).

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